Shade tolerance and the functional trait – demography relationship in temperate and boreal forests

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Running headline: Shade tolerance, functional traits and demography

SUMMARY

1. Despite being instrumental in forest ecology, the definition and nature of shade tolerance are complex and not beyond controversy. Moreover, the role it plays in the trait – demography relationship remains unclear.

2. Here, we hypothesize that shade tolerance can be achieved by alternative combinations of traits depending on the species' functional group (evergreen vs. deciduous species), and that its ability to explain the array of traits involved in demography will also vary between these two groups.

3. We used dimension reduction to identify the main trait spectra for 48 tree species, including 23 evergreens and 25 deciduous – dispersed across 21 genera and 13 families. We assessed the relationship between functional traits, shade tolerance and demographic performance at high and low light using structural equation modelling.

4. The dimensions found corresponded to the trait spectra previously observed in the literature and were significantly related to measures of demography. However, our results support the existence of a divergence between evergreen and deciduous species in the way shade tolerance relates to the demography of species along light gradients.

5. We show that shade tolerance can be attained through different combination of traits depending on the functional and geographical context, and thus its utilization as a

predictor of forest dynamics and species coexistence requires previous knowledge on the role it plays in the demographic performance of the species under study.

Keywords: boreal forests, demographic performance, functional ecology, structural equation modelling, temperate forests, trait spectra, tree life-histories, SORTIE

INTRODUCTION

Shade tolerance has been considered a fundamental axis of differentiation promoting species coexistence (Loehle 2000; Gravel *et al*. 2010) and explaining succession (Pacala *et al*. 1996; Ameztegui, Coll & Messier 2015). Despite this, and despite being instrumental in forest ecology, its definition and nature are complex and not beyond controversy (Valladares & Niinemets 2008; Lusk & Jorgensen 2013). Moreover, it is unclear what role general plant features such as shade tolerance play in the trait-demography relationship. Historically, shade tolerance has been considered a driver of the demographic performance of species, i.e. as a trait in itself, and thus several authors have assessed its relationship with performance indicators such as growth or survival (Walters & Reich 1996; Reich *et al*. 1998). Others, however, have considered shade tolerance as descriptor of ecological strategies and have thus contemplated shade tolerance as an integrative consequence of many interacting functional traits (Stahl *et al*. 2013; Reich 2014). Finally, some authors argue that shade tolerance should rather be considered as an aggregate trait or syndrome (i.e. an ill-defined integrative indicator of trait variation) that can be achieved by alternative combination of traits, depending on the ecological context, rather than an intrinsic species-specific property (Reich et al. 2003; Violle et al. 2007). Indeed, shade tolerance is known to vary depending on the ecological context, including ontogeny, the length of the growing season and the existence of other environmental stresses (Kneeshaw *et al*. 2006; Lusk *et al*. 2008; Valladares & Niinemets 2008).

Here, we evaluate these alternative conceptions of shade tolerance and hypothesize that it can be achieved by alternative combinations of traits depending on tree functional group

(deciduous vs. evergreen species), and that its ability to explain the complexity of traits involved in demography at low light environments will also vary between these two groups. We test these conjectures by assessing the relationship between a set of species-specific functional traits, shade tolerance and demographic performance for 48 well-studied tree species coming from temperate and boreal forests distributed worldwide across 10 different sites in 4 continents.

Functional traits are defined as morphological, physiological or phenological features of individuals that represent ecological strategies and determine how plants will respond to environmental factors (Violle *et al*. 2007; Pérez-Harguindeguy *et al*. 2013). By definition, traits should be ecologically meaningful and dictate the main demographic strategies of species. However, the direct link between functional traits and measures of plant performance such as growth or mortality has rarely been explicitly tested at large scales in temperate and boreal ecosystems, mainly due to the difficulty of having comparable species-specific data on both trait values and the main performance measures of individuals (but see Stahl *et al*. 2013; Adler *et al*. 2014; Paine *et al*. 2015). Functional traits are often grouped and represented by axes of trait variation called trait spectra, and the distribution of species along those axes is assumed to be indicative of their strategies for resource acquisition (Westoby *et al*. 2002; Reich 2014). We conducted dimension reduction methods to identify the main trait spectra, and then we used structural equation models (SEM) to assess how these spectra are related to shade tolerance and to plant performance at contrasting light conditions, with the aim of explicitly disentangling the role of shade tolerance in the trait-demography relationship.

Specifically, we expected that (1) functional traits co-vary along axes that broadly correspond to the main trait spectra already described in the literature (e.g. leaf, wood and seed economics spectra, Westoby *et al*. 2002); (2) the main trait spectra are good predictors of performance (growth and mortality); and (3) shade tolerance is related to different combinations of traits for different tree functional groups. We expect that linking species-specific demographic performance to functional traits and improving the understanding on the role that shade tolerance plays in the trait-demography relationship may open possibilities for constructing more general models of vegetation dynamics based on functional traits (**Error! Bookmark not defined.**Boulangeat *et al*. 2012; van Bodegom, Douma & Verheijen 2014) and therefore offer new avenues to answer current challenges in global ecosystem ecology.

MATERIALS AND METHODS

Study species and sites

One of the challenges faced when studying the relationship between functional traits and the demographic performance of species is getting the maximum number of comparable measures of whole-plant performance, which has traditionally limited the realization of studies at global scales. We obtained these measures of performance from the parameterization carried out in studies using the SORTIE model (Canham, Murphy & Papaik 2005). SORTIE is an individual-based, spatially explicit model of forest dynamics that to date has been parameterized at 11 study sites that cover a range of biomes from boreal to tropical forests (Fig. S1 and Table S1 in Supplementary Material). Since its creation in the 1990s, SORTIE has been parameterized for a total of 59 species – 32 evergreens and 27 deciduous – belonging to 23 different families (see Appendix S2 for a complete list of study species).

Tree functional traits

We mined the literature and various databases for species-specific values on functional traits for each study species. When possible, trait values were obtained from the same data source for all species. Since we could not find location-specific trait values for each species, we used mean trait values, ignoring intraspecific variation in functional traits. Interspecific variability in traits is commonly larger than within-individuals or between-population components, particularly for large environmental gradients such as the climatic gradient analysed here (Ackerly & Cornwell 2007; Martínez-Vilalta *et al*. 2010). When multiple values per species were found, we averaged the available values coming from the same biome. To reduce redundancy, we avoided the

126 selection of traits representing the same feature, but expressed on a different basis (e.g. mass-
127 based *vs.* area-based leaf traits, see Wright et al., 2004). Despite our best efforts, we had to
128 discard the species from the Luquillo forest at Puerto Rico (Uriarte *et al*. 2009), due to the lack
129 of standardized and comparable measures of traits. Also, only those traits available for at least
130 75% of the study species were retained. The final selection included 10 functional traits
131 representing leaf properties, seed mass, wood density and maximum tree height (Table 1), and 48
132 species. A complete list of the values of each trait for each species can be found in Table S3.

133 **Demographic performance: life-histories**

134 We collected low/high light growth and mortality for each species from the parameter values and
135 the functions of SORTIE available in the literature. In SORTIE, forest dynamics occur as the
136 result of the demography of every single individual in a plot. Demography results from three
137 main processes: growth, reproduction and mortality. Parameters are species-specific and
138 documented by extensive field sampling. Several equations describing these processes were used
139 at different sites. Moreover, each measure of performance can be governed by several parameters
140 that can co-vary and are often difficult to interpret. Thus, to better characterize the performance
141 of each species, we follow Pacala et al. (1996) and calculated demographic performance through
142 three 'life histories', i.e. standardized metrics of demographic performance that are easier to
143 interpret and allow comparison among species. Calculated life histories included growth at low
144 and high light availability as well as 5-year survival in low light (Table 1, and see Table S4 for
145 life history values for each species and site).

Data analyses

After combining all the compiled data, the final dataset contained 48 species for which complete information on functional traits and performance was available, including 23 evergreens and 25 deciduous, dispersed across 21 genera and 13 families. We extracted the main axes of trait variation in our dataset by running a principal coordinate analysis (PCoA) based on Gower's distance computed between pairs of species based on their functional traits. Gower's distance allows for the use of non-continuous data and PCoA admits pairwise missing values. We examined PCoA biplots to assess the distribution of species along the main identified axes of trait spectra. To understand which individual functional traits contributed to the identified main axes, we computed Pearson's correlation coefficients between trait values and the two major PCoA axes, as well as between species-specific values of demographic performance. Preliminary analyses showed that there were important differences in the results depending on leaf habit so we repeated the analyses three times: once for all the species pooled together, and then considering evergreen and deciduous species separately.

We used structural equation modelling (SEM) to test different hypotheses about the role of shade tolerance on the trait – demography relationship. SEM provides means for representing complex hypotheses about causal networks, and is particularly suited to account for factors that could conceptually be both causes and effects in the model structure (Shipley 2000, 2016). Within SEM, hypotheses are translated into a series of structural equations that can be solved simultaneously to generate estimated model covariance matrices. Each estimated model matrix is compared to the observed sample covariance matrix to determine whether the hypothesized model is an acceptable representation of the data. We used Chi-square tests to determine the

probability that the observed and expected covariance matrices differ by more than would be expected due to random sampling errors (Shipley 2000). If the data are consistent with the tested model, no significant differences between the observed and expected covariance matrices are expected. We considered an alpha value of 0.05 to determine statistical significance.

Specifically, we tested four alternative hypotheses about the role of shade tolerance, and each of them was translated into a conceptual model with its corresponding causal pathways (Fig. 1). A first hypothesis, named *full latent,* assumes that all correlations between the functional traits and the demographic variables are due to a common latent cause: shade tolerance (Fig. 1A). This model considers shade tolerance as a fundamental attribute of a species that causes both trait values and demographic properties. This model assumes that the observed correlations between the full set of functional traits and demographic variables are due to the fact that they are all responding to a single common cause (shade tolerance), and so the residual variation of each (the ε's) are mutually independent. A second model, named *latent trait*, assumes that shade tolerance is a latent trait that is jointly caused (but not entirely) by demographic variables, and which is in turn the single common cause of the observed traits (Fig. 1B). Because the demographic variables are causes, not consequences, of the latent, this conception of "shade tolerance" does not impose any necessary constraints on the patterns of covariation between these causes, and so the demographic variables are allowed to freely covary. The third model considered shade tolerance as a latent demographic property that is caused jointly by the traits, and which is the common cause for the demographic performance. This model, called *latent response*, allows some measurement error in the estimation of shade tolerance (Fig. 1C). Again, because the functional traits are causes, not consequences, of the latent "shade tolerance", the functional

traits are allowed to freely covary. Last, the *aggregate trait* model can be considered a modification of the third model, in which shade tolerance is jointly and completely driven by the traits (i.e. it assumes that there is no residual variance for shade tolerance).

Given the high correlation between most of the leaf traits in our dataset, we only included one of them (specific leaf area) in our model. To account for the potential variability in performance between regions due to their different climatic conditions (i.e. colder sites can be expected to be overall less productive than warmer sites), we removed the effect of climate (mean annual temperature and precipitation) from the demographic variables prior to including them in the analyses. To do so, we first fitted a model of performance as a function of climate, and then used the residuals into the SEM.

All variables were transformed where necessary (square-root or log-transformed) to meet normality assumptions, and the models were fit using maximum likelihood and the Satorra-Bentler robust estimator, which corrects for non-normality (Satorra & Bentler 1988). All the analyses were conducted in R version 3.0.3 (R Development Core Team 2014), and the *lavaan* package (Rosseel 2012). We set the measurement scale of the latent in model 1 by fixing its variance to unity, and set the measurement scales of the other models by fixing one of the path coefficients to unity. The R script for fitting these models is given in the supplementary information.

RESULTS

Main axes of trait variation as predictors of performance

When all the tree species were analysed together, the first axis of the PCoA accounted for 91% of the total variation in the matrix of distances based on functional traits (Fig. 2). Species were distributed along this axis in two clearly distinguishable groups. Deciduous angiosperms, with lower leaf longevity (mean = 5.2 months) but with higher SLA (154 $m^2 \cdot kg^{-1}$), photosynthetic capacity (133 mmol $CO_2\ g^{-1}s^{-1}$), and N content (2.1%), were located at one extreme of the spectrum, whereas evergreen gymnosperms (LL: 69 months; SLA: 61 $m^2 \cdot kg^{-1}$; Nmass: 1.2 %; Amax: 33 mmol $CO_2\ g^{-1}s^{-1}$) were located at the other extreme (Table 2; Fig. 1). Evergreen angiosperms, which in our study corresponded to evergreen broadleaf species from New Zealand's cool temperate rainforest, presented intermediate leaf characteristics, although they were located closer to the rest of the evergreen species. The second axis of trait variation explained a much smaller fraction (5.1%) of the total variability and was mainly related to wood density (WD). It was also more strongly related to performance measures than the first axis (Table 2).

For deciduous species alone, the variables related to the first axis were seed mass (SeM), LL and WD. This axis explained 70% of the variance, mainly separated small-seeded, fast-growing species such as *Betula* and *Populus* from the rest (Fig. 2), and was strongly correlated to all performance measures (Table 2). The second axis explained <10% of the variability and was related to SLA. For evergreen species, the first axis accounted for 60% of the variability and was related to WD and growth at full light (Table 2). The second axis explained <10%, and was related to SLA and Nmass, but not to performance measures.

The role of shade tolerance on the trait-demography relationship

The goodness of fit test indicated that the *latent response* and the *aggregate trait* model were consistent with the data for deciduous species, since the difference between the observed and expected covariation matrices was not statistically significant ($P = 0.393$ and $P = 0.394$, respectively; Table 3). However, upon convergence of the *latent response* model, the residual variance for shade tolerance was zero, thus in essence converting it into the *aggregate trait* model. According to this model, shade tolerance would be caused by a conjunction of high SLA, seed mass, wood density and maximum tree height. In turn, it would increase growth at both full and low light conditions, as well as survival in shade (Fig. 3A). The fact that the latent variable separates the traits from the demographic properties means that the functional traits combine together to affect the demographic properties rather than each trait separately affecting each demographic property.

In the case of evergreen species, the *latent trait* model was the only model consistent with the data (Table 3). According to this model, shade tolerance would be a latent trait jointly caused by demographic variables (in this case, only by growth at full light), and would in turn be the single common cause of the observed values of wood density. However, the statistical significance of the difference between the observed and expected covariation matrices was close to the defined threshold ($P = 0.057$) and only two of the coefficients were significantly different from zero, thus indicating lack of strong evidence for the existence of a latent variable.

DISCUSSION

The role of shade tolerance in the trait – demography relation

Our results support the existence of a divergence between evergreen and deciduous species in the way shade tolerance relates to demography, supporting the idea that shade tolerance shows convergent evolution (Paquette, Joly & Messier 2015), that is, the parallel adaptation of evolutionary distant species to the same condition (shade) but possibly using different strategies (traits). For deciduous species, our results argue against the consideration of shade tolerance as a functional trait per se, but rather as an aggregate property, i.e. an outcome of the combination and adaptation of several functional traits. This aggregation of traits, rather than each trait alone, then determines the demographic performance of the species. This model was rejected for the evergreen species, for which the *latent trait* model was the only model consistent with the data. However, the fact that the null probability of this latent trait model was close to the rejection threshold and, more importantly, that many of the predicted path coefficients were not significantly different from zero argue against accepting this model. For the evergreen species, the most parsimonious conclusion is that there is not a suite of demographic properties that together cause a suite of functional trait values. Rather, only one demographic property (growth at full light) is associated with only one functional trait (wood density), and it is not possible to determine the direction of causality for this bivariate pair.

Although the concept of shade tolerance is instrumental in forest ecology, its definition is complex and its relation to the demographic strategy of plants has generated some controversy (Valladares & Niinemets 2008). For instance, the 'carbon gain hypothesis' (Givnish 1988) states

that shade tolerance is mainly related to the ability of plants to maintain positive growth rates even in light-scarce environments, while the 'high-light growth / low-light survival trade-off' (Kobe *et al*. 1995) predicts a negative correlation between growth rates at high light and survivorship in low light. However, both hypotheses have been challenged (Walters & Reich 1999; Gravel *et al*. 2010), and there is a growing body of evidence showing that the ability to tolerate shade can be achieved by alternative combinations of physiological, morphological and architectural traits that can be species- and environment-specific (Delagrange *et al*. 2004; Valladares & Niinemets 2008; Ameztegui & Coll 2011). Interestingly, we found a positive relationship between growth and survival in low light for deciduous species (Pearson's $r = 0.50$; Table S4.2), whereas survivorship in low light was negatively related to growth at high light for evergreens ($r = -0.60$), suggesting a divergence in the growth-survival trade-off. A recent study reported a similar conifer–angiosperm divergence in the growth vs. shade tolerance trade-off for temperate rainforests in New Zealand (Lusk, Jorgensen & Bellingham 2015). Our results indicate that this divergence may be generalizable to other temperate and boreal forests.

The divergence between deciduous and evergreen tree species, and the poorer relationship of shade tolerance to performance for the latter group have been previously related to the need for conifers to better resist desiccation and/or frost damage due to their early-successional status (Lusk *et al*. 2015). Although poly-tolerance, i.e. the ability of a species to simultaneously tolerate two or more stresses, is not common due to universal physiochemical constraints, recent studies show that the ability of species to tolerance shade and drought at the same time is favoured at long growing seasons (Laanisto & Niinemets 2015). Most of the evergreen species studied here thrive in boreal or subalpine areas with shorter growing seasons than in temperate biomes, which

could explain the observed inability of conifers to simultaneously withstand low-light and low-water environments, and would also explain the lack of strong correlations between shade tolerance and demographic performance for this functional group.

Main spectra of functional traits and predictors of performance

Although shade tolerance has been a cornerstone for the study of forest dynamics in temperate areas, Gravel *et al*. (2010) showed that it alone is not sufficient to explain the stable coexistence of several tree species. In our dataset, wood density emerged as independent from shade tolerance and as a good predictor of performance for deciduous species, suggesting that more than one dimension is needed to explain the dynamics of these forests (Loehle 2000). For evergreen species, wood density was also the only variable related to growth at full light, thus stressing its importance for both functional groups. Wood density is considered an integrator of several wood properties, and is increasingly being regarded as a key functional trait by ecologists (Chave *et al*. 2009; Wright *et al*. 2010). A greater wood density is related to resistance to hydraulic failure and survival (Muller-Landau 2004; King, Davies & Noor 2006; Poorter *et al*. 2010), but also to greater construction costs, and negative relationships between wood density and growth rates have been observed in different ecosystems (see, for example, Nascimento *et al*. 2005; Poorter *et al*. 2008; Chao *et al*. 2008; Martínez-Vilalta *et al*. 2010).

Contrary to wood density, the leaf economics spectrum alone was a poor predictor of species' performance. The existence of a leaf economics spectrum along which the species are distributed as a function of their resource investment is widely acknowledged (Wright *et al*. 2004; Poorter & Bongers 2006; Osnas *et al*. 2013), but its role as predictor of plant performance has raised more

313 debate, particularly for non-tropical ecosystems (Martínez-Vilalta *et al*. 2010; Stahl *et al*. 2013;
314 Paine *et al*. 2015). It has been recently suggested that leaf traits may be poor indicators of life
315 history strategies in some geographic areas due to their high phenotypic plasticity (Funk &
316 Cornwell 2013).

317 **Potential shortcomings and future research directions**

318 Some constraints to our approach are worth discussing. For instance, we used mean trait and
319 performance values for each species, ignoring between-population variation in both functional
320 traits and demography. However, interspecific variability in functional traits is commonly larger
321 than within-individuals or between-population components, particularly over large spatial or
322 environmental scales such as the one used for this study (Ackerly & Cornwell 2007; Martínez-
323 Vilalta *et al*. 2010; Laforest-Lapointe, Martínez-Vilalta & Retana 2014).

324 Despite the considerable efforts needed to amass this data, it is still a small data set with limited
325 statistical power. It only contained a few evergreen angiosperms, and no deciduous
326 gymnosperms. A more complete and balanced dataset would allow to test the generality of our
327 results across biomes, but the challenge is to have comparable performance measures for such a
328 database. Moreover, splitting the database into deciduous and evergreen species is a dichotomous
329 definition of a continuous process: leaf lifetime, which is often considered a foundational
330 component of the leaf economics spectrum. Although there are important differences between
331 these two groups that expand much beyond the leaf lifespan, this division is highly
332 phenomenological because it does not allow us to pin point the trait that is responsible for this

split. Future research could examine how shade tolerance may vary along a continuous axis of leaf lifespan, and the implications of such a variation.

Last, our functional trait dataset was mainly composed of leaf or whole-plant measurements, as they are the most easily found in the literature. Although the importance of leaf traits and their links to ecosystem functioning are beyond any doubt, the importance of other organs such as wood or roots is increasingly being recognized (Moles & Westoby 2006; Chave *et al*. 2009; Mommer & Weemstra 2012), and whole-plant architectural traits such as crown depth or canopy light transmittance are known to be particularly well related to shade tolerance (Valladares & Niinemets 2008). Our results indicate that leaf traits alone are not enough to predict demographic performance for the studied species, and thus including a more complete set of non-leaf traits should be explored in the future.

Conclusions

Overall, we found that the main dimensions of tree functional traits corresponded to the trait spectra previously observed in the literature, as hypothesized by Westoby *et al.* (2002) and Reich (2014). The trait spectra were significantly related to measures of demographic performance (growth and survival) for 48 tree species from temperate and boreal forests. Our results also support the existence of a divergence between evergreen and deciduous tree species in the way shade tolerance relates to the demography of species along light gradients, which can be due to the simultaneous existence of other environmental stresses not accounted for. Thus, shade tolerance should be used with caution when attempting to predict the demography and coexistence of species based on their functional traits. Therefore, if general models of vegetation

354 dynamics based on functional traits are to be constructed (Boulangeat *et al*. 2012; van Bodegom,
355 Douma & Verheijen 2014), shade tolerance should not be used at a global scale without prior
356 knowledge of its role in the dynamics of the communities to be modelled.

357 **ACKNOWLEDGEMENTS**

358 The authors acknowledge Dr. Yoshida and Dr. Evans for kindly providing the SORTIE
359 parameters for species from Japan and United Kingdom, respectively. We are also grateful to
360 Timothy Paine and two anonymous referees for their constructive comments on an earlier
361 version of this manuscript. This research was supported by a Juan de la Cierva Fellowship to
362 A.A. (FJCI-2014-20739), a NSERC Strategic Grant to D.G. and the NSERC industrial Chair
363 program to C.M. The authors declare no conflict of interests.

364

365 **AUTHORS' CONTRIBUTIONS**

366 • Conceived and designed the experiment: AA, AP, CM, DG
367 • Acquired and analyzed the data: AA, AP, BS, MH
368 • Interpreted the results: AA, AP, BS, MH, CM, DG
369 • Wrote the paper: AA, AP, BS, MH, CM, DG

370

DATA ACCESIBILITY

- Study sites and species descriptions: uploaded as online supporting information (Tables S1, S2).

- All demography and functional trait data used in this study are available from the Dryad online database (doi:10.5061/dryad.12b0h). The data sources for the values are uploaded as online supporting information (Table S3).

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TABLES

Table 1 Selected variables (functional traits and demographic performance), units and descriptive statistics (mean ± SD) for the 48 tree species split by leaf habit (23 evergreen vs. 25 deciduous). P-values indicate significance of the differences in the variable values between deciduous and evergreen species, based on t-tests

Abbr.	Trait	Levels / units	Deciduous	Evergreen	*P*
Functional traits					
Lhab	Leaf habit	Deciduous/ Evergreen			
SLA	Specific Leaf Area	$m^2 \cdot kg^{-1}$	154.1 ± 50.0	62.1 ± 25.4	< 0.001
Amax	Photosynthetic capacity per unit leaf mass	$mmol \cdot CO2 \cdot g^{-1}s^{-1}$	133.1 ± 41.8	35.4 ± 15.8	< 0.001
Nmass	Leaf N content per unit mass	%	2.14 ± 0.28	1.20 ± 0.27	< 0.001
Pmass	Leaf P content per unit mass	%	0.20 ± 0.06	0.13 ± 0.05	< 0.001
LL	Leaf lifespan	months	5.2 ± 0.8	65.2 ± 30.6	< 0.001
Llength	Leaf length	mm	111.6 ± 63.2	34.3 ± 32.2	< 0.001
SeM	Seed mass	$mg \cdot seed^{-1}$	424.1 ± 934.6	30.6 ± 105.7	0.047
WD	Wood density	$g \cdot cm^{-3}$	0.51 ± 0.09	0.44 ± 0.16	0.084
MaxH	Maximum height	m	24.4 ± 8.1	30.1 ± 10.3	0.042
Demographic performance: life histories					
Growth-L	Time needed for a sapling with DBH= 1cm to become an adult (DBH=7.5 cm) when light = 100%	Years	17.1 ± 8.1	34.8 ± 39.2	0.039
Growth-D	Time needed for a sapling with DBH= 1cm to become an adult (DBH=7.5 cm) when light = 1%	Years	244.6 ± 255.2	489.5 ± 619.1	0.078
Surv-D	5-year survivorship of a sapling with DBH= 1cm when light = 1%	%	0.42 ± 0.38	0.33 ± 0.36	0.341

539 **Table 2**. Pearson's correlation coefficient (r) between functional traits, demographic
540 performance and the first two axes of principal coordinate analyses (A1, A2) for all the data
541 analysed together and separated into deciduous (D1, D2) and evergreen (E1, E2) tree species,
542 respectively. Also shown are the percentages of the variance explained by each pair of two PCoA
543 axes.

	All together		**Deciduous**		**Evergreen**	
	A1 90.9%	A2 5.1%	D1 69.7%	D2 9.6%	E1 60.2%	E2 9.6%
Functional traits						
SLA	0.90***	0.48***	0.24	0.63***	-0.55*	-0.68***
Amax	0.84***	0.44*	-0.44	0.47	-0.63*	-0.43
Nmass	0.89***	0.24	-0.09	0.13	0.01	-0.79***
Pmass	0.77***	0.04	0.00	-0.24	0.06	-0.26
LLifespan	-0.92***	-0.35	0.80***	-0.33	0.47	0.07
LLength	0.78***	0.23	0.41	-0.30	-0.02	-0.02
SeM	0.41*	0.24	0.87***	-0.15	0.13	-0.61*
WD	0.32	0.91***	0.73***	0.04	-0.88***	-0.09
MaxH	-0.25	-0.41*	0.10	-0.42	0.52	-0.24
Demographic performance						
Growth-L	-0.34	0.56***	0.56**	0.11	-0.83***	-0.23
Growth-D	-0.27	-0.23	-0.76***	-0.01	0.08	0.27
Surv-D	0.12	0.18	-0.58**	0.06	-0.04	0.01

544

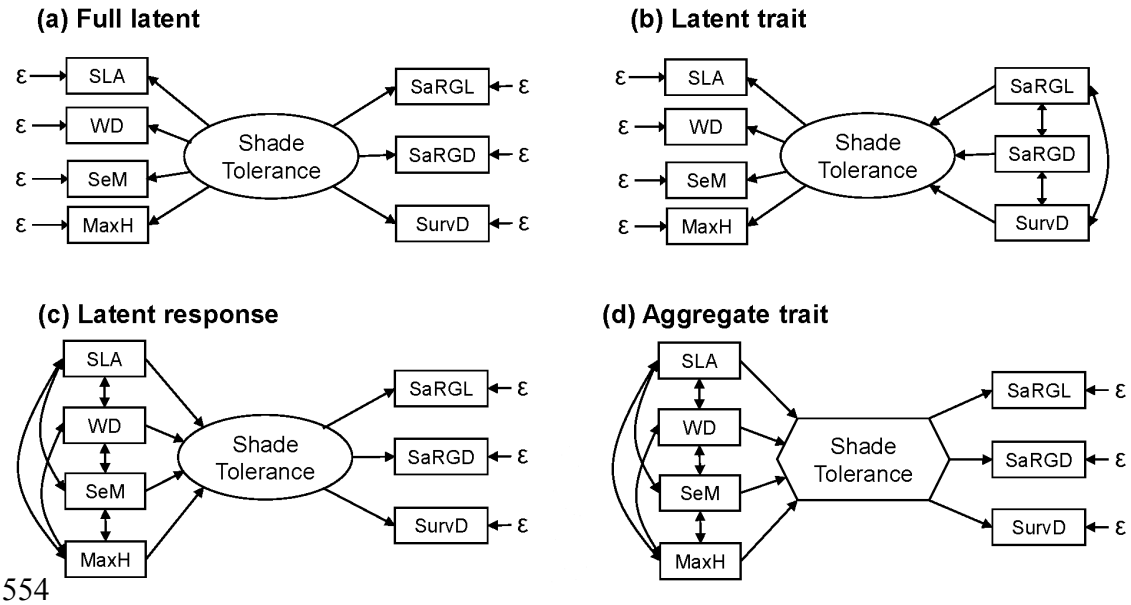
545 **Table 3**. Summary output for the fit of SEM models for deciduous and evergreen tree species.
546 Four models were assessed for each group, to test the alternative hypotheses about the role of
547 shade tolerance in the functional trait – demography relationship. The best fit model for each
548 group is indicated in bold. Please see Figure 1 and the main text for a complete description of the
549 alternative pathways.

	Deciduous			**Evergreen**		
	χ^2	df	*P*	χ^2	df	*P*
Model (a) Full Latent	25.586	14	0.029	27.500	14	0.017
Model (b) Latent Trait	37.049	14	0.001	**23.228**	**14**	**0.057**
Model (c) Latent Response	**8.430***	**8***	**0.393***	21.124	8	0.007
Model (d) Aggregate Trait	**9.484**	**9**	**0.394**	24.554	9	0.004

550

551 * Model c converged for deciduous species but, upon convergence, residual variance for the
552 latent was zero, thus converting it to model d.

553 **FIGURES**



554

555 **Fig. 1.** Conceptual models explaining alternative pathways to describe the role of shade
556 tolerance in the functional trait – demography relationship for temperate and boreal forests.
557 SLA, WD, SeM, MaxH are functional traits; whereas SaRGL, SaRGD, SurvD are life
558 history variables of demographic performance (see text). Four alternative conceptual
559 models were tested: (a) *full latent model*, which assumes all correlations between the traits
560 and the demographic variables are due, but not completely, to a common latent cause
561 (shade tolerance); (b) *latent trait model*, where shade tolerance is a latent trait caused
562 jointly by the demographic variables, which in turn is the single common cause of the
563 correlated traits; (c) *latent response model*, where shade tolerance is a latent demographic
564 property caused jointly (but not completely) by the traits, and which is the common cause
565 of all of the demographic variables; (d) *aggregate trait model*, where shade tolerance is
566 jointly and completely (i.e. no residual variance) caused by the traits, and causes variation
567 in demographic variables.

568

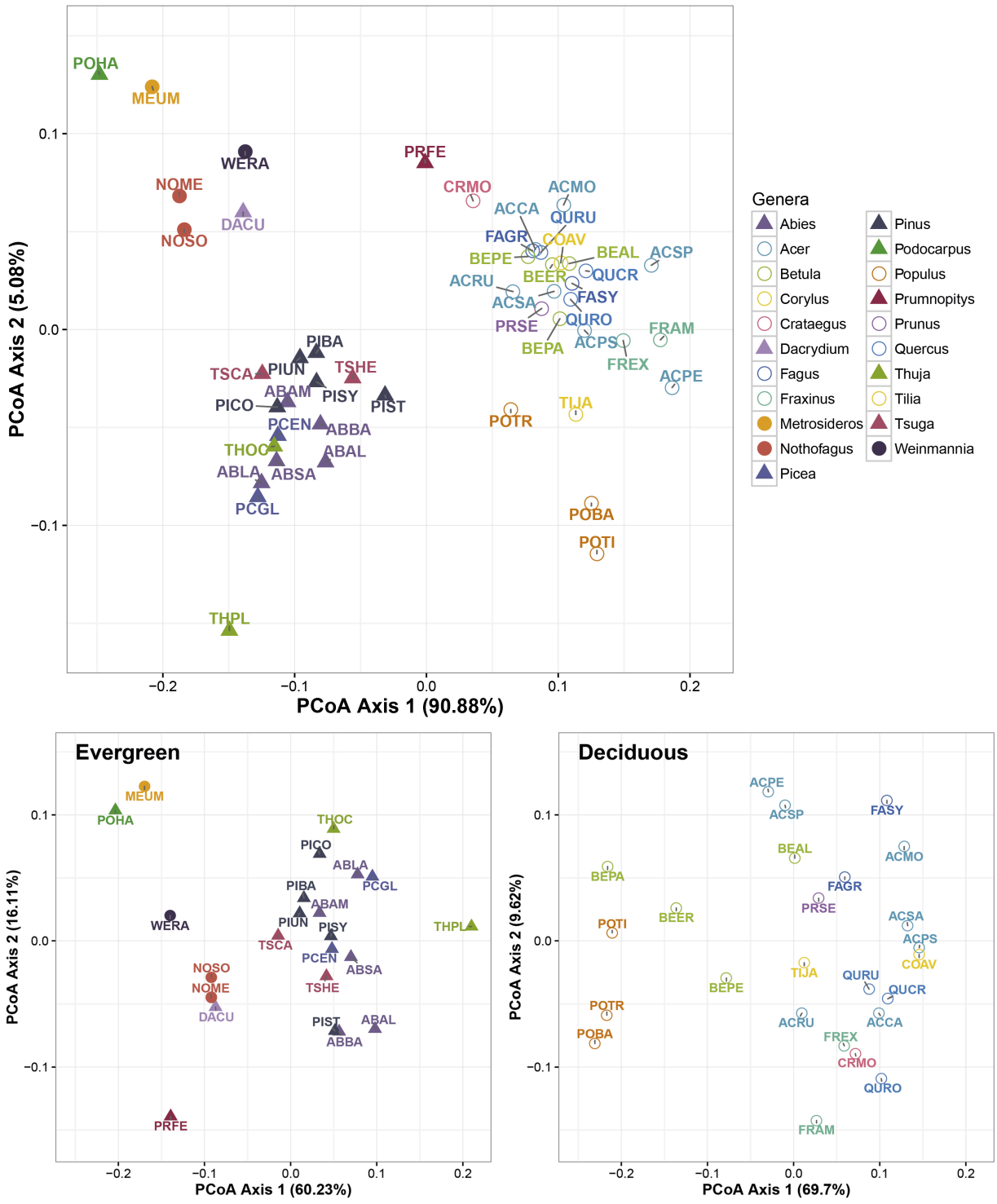


Fig. 2. PCoA ordination showing Gower's distance among 48 tree species based on 10 functional traits when analyzed together (top panel), and when separated into evergreen

572 (n=23) and deciduous (n=25, bottom panel). Symbols represent the combination of
573 phylogeny and leaf habit: evergreen gymnosperms (full circles); deciduous angiosperms
574 (open triangles) and evergreen angiosperms (full triangles). When all species are analysed
575 together, the first axis explains 90.9% of the variability in the distance matrix and clearly
576 separates evergreen gymnosperms (full circles) from deciduous angiosperms (open
577 triangles). Points with the same colour correspond to species of the same genus, as
578 indicated in the legend. The 4-letter code indicates species (see Table S2).

579

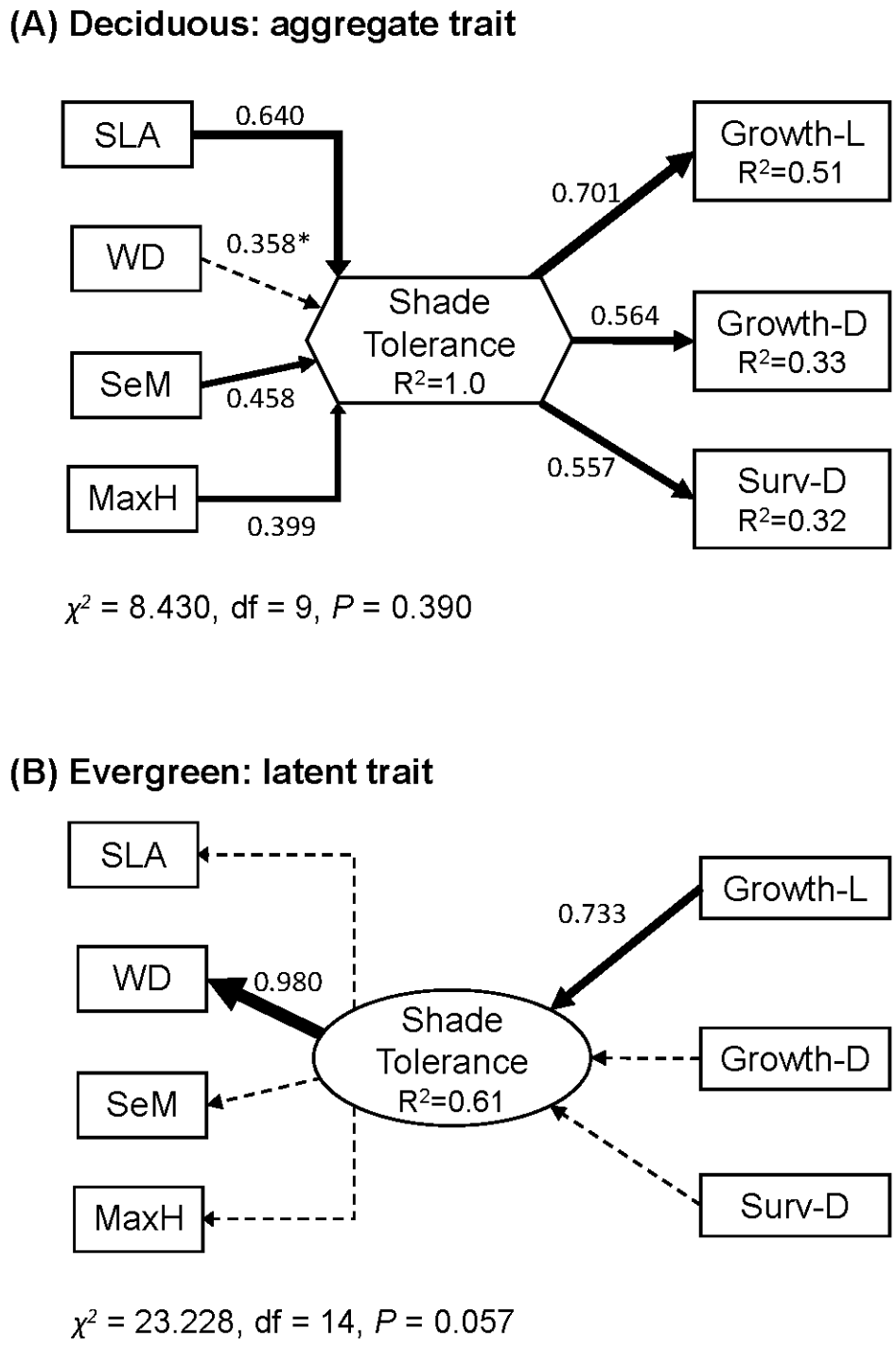


Fig. 3. Structural equation models (SEM) explaining the best-fit pathway to describe the role of shade tolerance in the functional trait – demography relationship in temperate and boreal forests.

583 For deciduous tree species the best model considered shade tolerance as an aggregate trait caused
584 jointly and completely by the traits, and which causes variation in demographic variables. For
585 evergreen tree species, the best fit model considered shade tolerance as a latent trait caused
586 jointly by demographic variables, and which is the single common cause of the correlated traits.
587 Standardized coefficients based on the correlation matrix are shown for each path. Dotted lines
588 represent non-significant effects, and line thickness is proportional to their relative weight.
589 Asterisks beside the coefficient indicate significance at the $P < 0.10$ level. R^2 is shown beneath
590 the variable names. The chi-square statistic (testing significant differences between the observed
591 and expected covariance matrices), degrees of freedom (df), and *P* (based on likelihood-ratio
592 test) are also shown.